INHERITANCE OF WILDNESS AND TAMENESS IN MICE[1]

WALKER MYRICK DAWSON

University of Illinois, Urbana, Illinois

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INTRODUCTION

Races and strains of domestic animals as well as individuals within a group often differ to a marked extent in temperament and reaction to a given situation. These differences are, in many cases, of considerable economic importance. For example, some breeds of chickens are much more excitable than others, draft horses generally have much quieter dispositions than race horses, dairy cows are as a rule more nervous and "temperamental" than beef cattle. Unfortunately little work has been done in studying the mode of inheritance of characters of this type.

[1] Paper No. 43 from the Division of Animal Genetics, Department of Animal Husbandry, UNIVERSITY OF ILLINOIS, part of a thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Animal Husbandry in the Graduate School of the UNIVERSITY OF ILLINOIS, 1931. The author wishes to express his appreciation to Doctor ELMER ROBERTS under whom the experiment was conducted and also to Professor C. M. WOODWORTH who assisted with the problem during Doctor ROBERTS' absence in China, 1929–30.

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The purpose of this investigation was to determine whether genetic factors are involved in wildness and tameness in mice and if so the mode of their inheritance. In this experiment the length of time required by a mouse to travel a given distance under the conditions specified was taken as a measure indicating the degree of wildness or tameness. The use of these terms does not imply that the writer believes that the measure used in this study measures to the full extent wildness and tameness. These phenomena are very complex and the best that can be done is to measure some manifestations of them. This YERKES and COBURN did through observation and the writer has attempted to do by measuring the reaction of running under the conditions specified (p. 299 in which a significant difference existed between wild and domesticated strains).

It seems reasonable that wild mice have been selected for wildness by the process of natural selection and that tame mice have been selected for tameness by the process of domestication. Thus one would expect if wildness and tameness are inherited that there would be a tendency for the wild mice to be homozygous for the genes for wildness and the domesticated mice homozygous for the genes for tameness.

MATERIALS

There were two quite distinct types of mice in regard to their reactions available for a study of this kind: (1) the so-called wild mice found in barns and houses, and (2) the so-called tame mice sold by fanciers. The mice used to obtain stock for this experiment came from the following sources:

Wild mice

All of the wild mice came from a strain which had been reared for several years by Doctor ELMER ROBERTS in the Animal Genetics Laboratory of the UNIVERSITY OF ILLINOIS. These mice were all descendants of mice caught in the wild state at a considerable distance from the laboratory. They were easily excited and would run rapidly about their cage or hide in the paper when their pen was disturbed. When picked up they invariably struggled and tried to escape often biting the forceps or gloved hand with which they were held. If allowed to escape on the floor they would immediately dash for safety under the furniture or into a corner of the room. Sixteen pairs were used.

Tame mice

The tame mice were of three strains:

Albinos—Three males and twelve females were obtained from a fancier in New York City.

Pink eyed short eared browns—Two males and thirteen females were obtained from Professor W. H. Gates at Louisiana State University.

Pink eyed browns—a pair of these was obtained from Dr. Elmer Roberts. They came from a strain that had been maintained in the laboratory for a number of years.

The mice in these three tame strains varied considerably in their reactions to being disturbed or caught but in general their motions were slower than those of the wild mice. They often did not attempt to hide and were much less likely to struggle or bite when caught. When placed on the floor they generally sniffed about curiously but did not run away as did the wild mice.

METHODS

Care of the animals

All of the mice were cared for in as nearly the same manner as possible throughout the experiment. The handling of the animals, in addition to testing them to determine their reaction, consisted in that necessary for weaning the young and for the transfer of mice in breeding operations. When matings were made between parents from strains which reacted very differently in the runway the male was always removed before the young were born or within one or two days after their birth. The breeding pens were inspected every day when young were expected. When the young were a month to six weeks old, they were weaned and records made of their color, sex, and length of ears where this character was involved. Young mice of the same sex were placed together in a separate pen until after completion of tests. Individuals from two or more litters were sometimes placed in the same cage, although mice that were expected to differ widely in their reaction in the runway were always placed in separate pens.

In handling the adult or partly grown mice during the above procedure and also during the tests, we caught the animals by the tail with a pair of placental forceps. If they were inspected or marked they were held in the gloved hand. Five-gallon tin cans with a few inches of shredded paper in the bottom were used as receptacles for the mice during the tests, when weaning the young and when making up matings.

Testing the mice in the runway

The method of testing consisted in placing the mouse at one end of a runway and allowing it to run to the other end. The time required was recorded by means of a stop watch.

The runway was 24 feet long, 9½ inches wide and 13 inches high. The sides and ends were of galvanized sheet iron, the floor of soft wood. One foot from each end a black line was painted on the floor of the runway. The time required for the mouse to run from one line to the other, a distance of 22 feet, was recorded. A movable partition made of wallboard and bound with rubber was used to prevent the mouse from running back during the test and to aid in starting the test and capturing the mouse afterward.

The following procedure was carried out in testing the mice in this device. On the date that the mice in a certain pen were to be tested they were carried to the runway a short distance away and tested one at a time. The mouse to be tested was confined by the movable partition in a space about one foot from the end of the runway until everything was ready when the partition was raised and the stop watch started as soon as the mouse crossed the black line. The mouse was followed by the experimenter with the partition which was placed in position to prevent the animal from running back if it showed any signs of doing so. Nothing was done to frighten the mouse other than the procedure described. This was usually sufficient to cause even the tame mice to run or walk toward the other end of the runway. If the mouse ran swiftly, it was impossible to keep up with it with the partition; but if more slowly the partition was moved along and kept about twelve to fifteen inches behind the mouse. If the mouse stopped and showed no inclination to go forward the partition was slowly advanced until it touched the mouse. In all but three or four cases this was sufficient to start the mouse again. The few individuals where this was not the case were shoved a little and thus started. When the mouse crossed the line at the far end of the runway the watch was stopped and the partition taken out of the runway allowing the mouse to run back to the starting point or in case it did not do so voluntarily it was urged by means of the partition. This prevented the mice from associating the far end of the runway with being caught. Since each individual was tested three times this point was of considerable importance.

After the mouse had been cornered at the starting point by means of the partition, it was caught and the number in its ear read. The length of time required to run the 22 feet was then recorded together with any notes deemed necessary. When all the mice in the pen had thus been tested, they were taken back into the room where they were permanently kept and weighed individually to the nearest quarter of a gram.

Each mouse in the experiment was tested by the above method three times. These trials were conducted at weekly intervals after the mouse reached 75 days of age. In order to facilitate the testing and caring for the mice, a variation of one day in either direction was permitted. Thus the first trial for a given mouse might occur on the 74th, 75th or 76th day. A few trials had to be made on different dates.

The trials were in nearly all cases made in the evening or at night when there was very little outside disturbance to distract the mice. The lighting was kept as far as possible the same throughout the experiment.

Selection and mating of breeding stock

Mice of the various stocks described on page 297 were mated and the young raised under the conditions in the laboratory to produce the parental individuals used in the experiment. These animals have been designated as first generation wild and first generation tame. As an aid in selecting breeders to use in crosses a preliminary study was made of the spread and nature of the population curves of the wild and tame strains. The average of the three trials in the runway was used as the basis of selection throughout the experiment. Other factors, however, were considered such as the health of the individual, nature of the matings, spread of the items making up the average or anything which indicated that the average might not truly represent the genetic constitution of the individual.

Breeders to be used in producing F_1's were chosen from the fastest and slowest parts of the wild and tame distributions respectively (figures 1 and 2). In the wild strain breeders were selected that ran the distance in less than six seconds while in the tame strain they were selected from those that had a record of twenty seconds or slower. It was believed that by this procedure there would be a tendency to select individuals more nearly homozygous for the factors controlling the reaction than there would be if individuals were selected at random in case the population of the strain contained heterozygous individuals. If, on the other hand, the strain were homozygous, no harm would be done by the selection.

Reciprocal matings were used in producing the F_1's. After a considerable number of individuals were obtained a study was made of their distribution with regard to their reaction in the runway in order to determine the proportion of individuals at various parts of the distribution. F_2's were produced from a group of F_1's selected from the whole F_1 population in such a manner that the proportion of mice having a certain average test in the runway would conform as nearly as possible to that in the entire population. Backcrosses were made between F_1's which varied in the degree of their reaction and both parental strains. A number of female individuals from $F_1 \times$tame were mated back to tame males, often to their sires. This formed in reality a progeny test of the females. Matings were made between individuals from various parts of the F_2 population, and the progeny tested in some cases for several generations.

Inbreeding was avoided as much as possible in the production of the first generation wild, first generation tame, F_1's and F_2's. The descendants of the various tame strains were kept separate in crosses; for example, F_1's from wild × albino were always mated to F_1's from wild × albino in producing the F_2's.

RESULTS

The results given were obtained over a period of three and a half years from the fall of 1926 to the spring of 1930. Two thousand three hundred seventy-six mice were born in the experiment and of these one thousand five hundred seventy-five were raised to maturity and tested in the runway. Nearly all of these entered into the results presented, although some on which complete records could not be obtained or which were derived from special crosses, as $F_2 \times F_3$, have been omitted.

Very little if any difference was found between the tame strains. In most cases they have been considered together in the results, although in a number of instances only the albino strain has been used. More than two-thirds of the tame population in the first generation were albinos. They proved much more vigorous and prolific than either of the other tame strains and for this reason were used to a greater extent.

Reliability of test

The reliability of the runway test appears to be satisfactory, at least when the results from all the mice are judged by (1) correlating the different trials with each other and (2) obtaining the coefficient of reliability by use of the Spearman Brown formula.[2] SHEN's (1924) formula was used to compute the probable errors of the reliability coefficients[3] (tables 1 and 1a).

The distribution of the mice in scatter diagrams for the correlation between the trials for all the mice indicates that the correlation is rectilinear or nearly so. Correlation ratios were worked out for the wild males first generation for the three trials in the runway.[4] Correlations of all except the third trial on the first satisfied the Blakeman test (REITZ 1927), and this exception exceeded the limit set by BLAKEMAN by only a small amount.

[2] Spearman Brown formula: $R = ar/1 + (a-1)r$ in which R = the coefficient of reliability when the original test is used (a) times; r = the average of the correlation coefficients of the (a) trials. (KELLEY 1923, ODELL 1930.)

[3] $P.\ E._R = 0.6745\ a(1-r)^2/\sqrt{N}[1-(a-1)_r]^2$ (SHEN 1924).

[4] $\eta_{12} = 0.738$ $\eta_{13} = 0.618$ $\eta_{23} = 0.860$
$\eta_{21} = 0.848$ $\eta_{31} = 0.712$ $\eta_{32} = 0.838$

TABLE 1

Reliability of the runway test for various groups of mice.

GROUP	NUMBER OF MICE	COEFFICIENT OF RELIABILITY*
All mice used	1232	0.921±0.003
All ♂♂	614	0.927±0.004
All ♀♀	618	0.923±0.004
Wild and Albino first generation ♂♂	82	0.957±0.007
Wild and Albino first generation ♀♀	88	0.967±0.007
Wild first generation ♂♂	43	0.827±0.038
Albino first generation ♂♂	39	0.709±0.071
Wild first generation ♀♀	47	0.866±0.028
Albino first generation ♀♀	41	0.873±0.028

* See footnotes 2 and 3 for the formulas used.

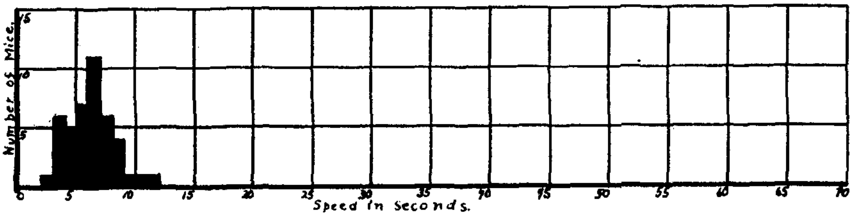
TABLE 1a

Correlation coefficients between the three trials in the runway for various groups.

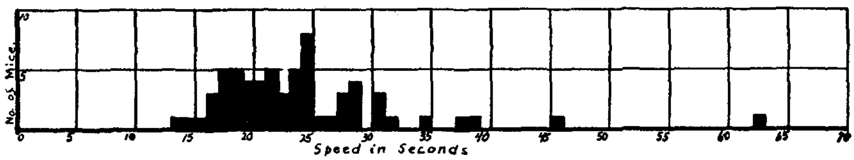
GROUP	TRIALS CORRELATED			
	NUMBER OF INDIVIDUALS	FIRST WITH SECOND TRIAL	FIRST WITH THIRD TRIAL	SECOND WITH THIRD TRIAL
All mice used	1232	0.788±0.007	0.759±0.008	0.841±0.006
All ♂♂	614	0.810±0.009	0.788±0.010	0.827±0.009
All ♀♀	618	0.764±0.011	0.750±0.012	0.885±0.006
Wild and Albino first generation ♂♂	82	0.878±0.017	0.851±0.021	0.915±0.012
Wild and Albino first generation ♀♀	88	0.909±0.012	0.883±0.016	0.929±0.010
Wild first generation ♂♂	43	0.687±0.054	0.390±0.087	0.790±0.039
Albino first generation ♂♂	39	0.403±0.090	0.267±0.100	0.676±0.059
Wild first generation ♀♀	47	0.676±0.053	0.658±0.056	0.716±0.048
Albino first generation ♀♀	41	0.696±0.054	0.599±0.068	0.791±0.039

Parental strains

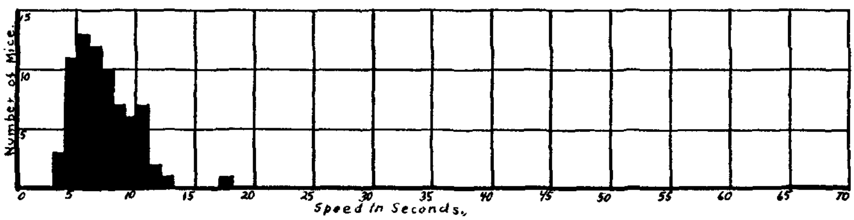
The results of testing the first generation wild and first generation tame in the runway are given in tables 2 and 3 and figures 1 and 2. (Animals of the first generation are unselected, see page 300.) These are for the average of three trials. The tables and figures show that there is a marked difference between the wild and tame strains. A comparison of the means shows that the difference is more than 24 times its probable error. There is no overlapping in the males and very little in the females. The variability of the wild is very much less than that of the tame. A study of the difference between the sexes, given in table 3, shows that in the wild strain the females are significantly faster than the males, while in the tame strains the difference is not significant except in the first trial for the albinos. In



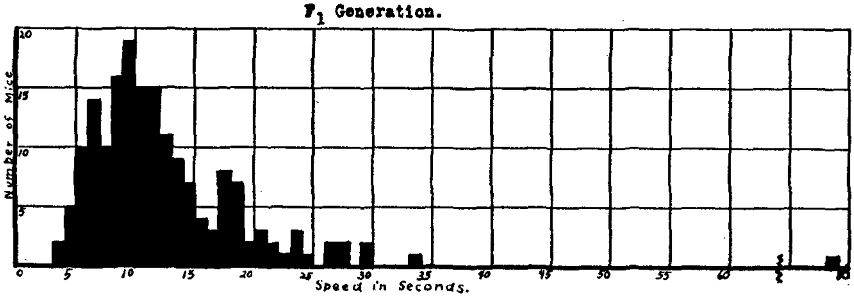
Wild First generation.



Tame First Generation.



F_1 Generation.



F_2 Generation.

FIGURE 1.—Distribution of males in runway test. Average of three trials.

this case the males are significantly faster than the females. The smaller number of animals in the pink eyed short eared brown strain probably accounts for the difference not being significant in that case.

The distributions of the wild and albino tame strains for the first generation in the first, second and third trials in the runway are given in

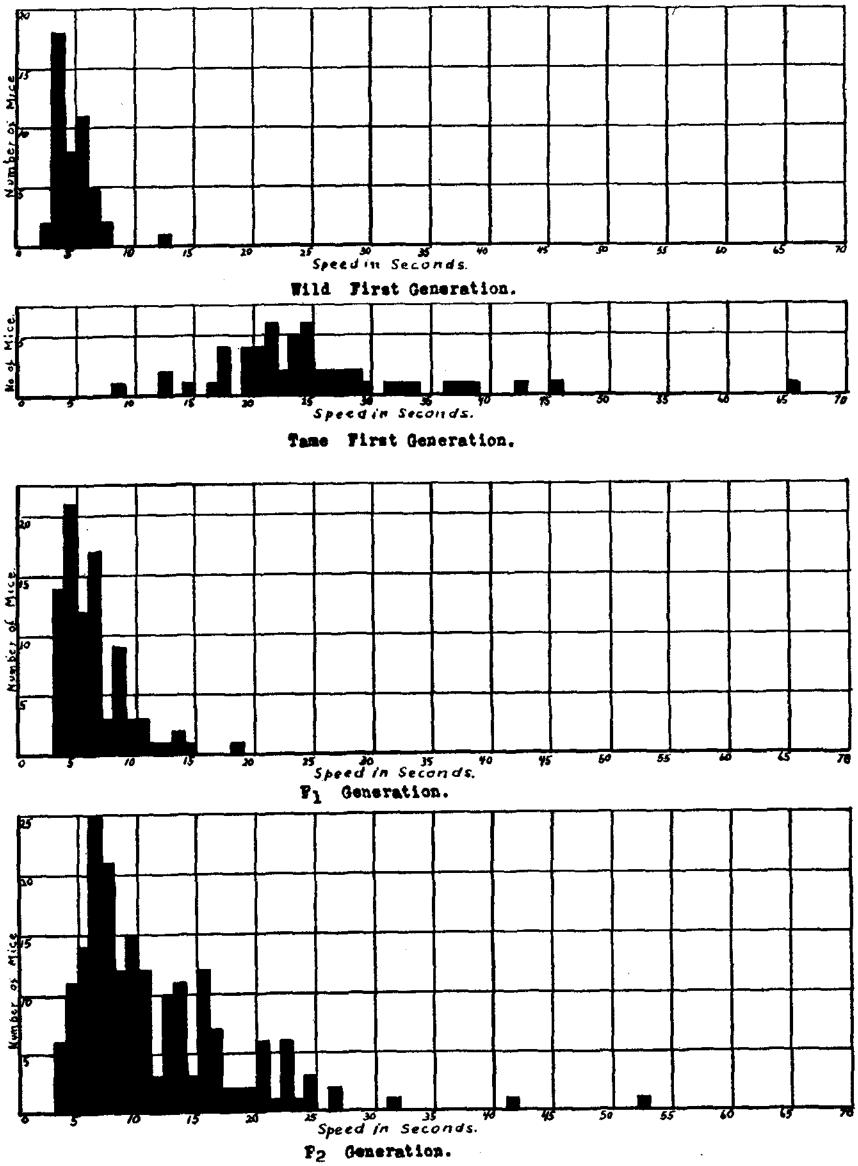


FIGURE 2.—Distribution of females in runway test. Average of three trials.

table 5. It is interesting to note that the mean speed in each case is lowest in the first trial and increased in the second and third trials. In the tame

strains the difference between the first trial and the second and third trials is very marked and is proportionally about twice as large as in the wild strain.

The correlations between the trials as shown by the correlation coefficients in table 1a are fairly high. When the wild and tame stocks are treated as one population the correlation between the trials is greater than when the wild and tame stocks are considered separately, that is as two populations. This difference can be explained upon the basis of the existence of unlike sub populations in the combined table which in this case are the wild and tame strains.

Weight and age were found to have little effect on reaction when studied with the wild and albino strains in the runway.

F_1 *generation*

The distribution of F_1's produced from crossing selected individuals of the wild and tame strains (described under Methods, page 300) is given in tables 2 and 3 and figures 1 and 2. The reaction of the wild mice was found to be almost completely dominant over the reaction of the tame mice. The mean for the F_1's showed them to be very little slower than the wild. While the variability of the F_1's was slightly greater than that of the wild, the population was quite uniform. The difference between the sexes (table 3) was not significant. However, it is interesting to note that the mean for the females is slightly less than that for the males.

No difference that could be considered significant was found between F_1's from reciprocal crosses. A comparison of the means is given in table 6. The fact that no difference existed between the young from the two types of matings shows that the association with the mother had had practically no effect on the speed of the offspring.[5] At least the offspring of of tame mothers mated to wild males tested much faster than their mothers. Also, as will be seen later, fast F_1 females produced some slow F_2 offspring, thus proving that the results obtained can not be accounted for by the influence exerted by the association of the young with parents of different degrees of reaction in the runway.

F_1 matings were studied individually to see whether the degree of reaction shown by the F_1 parents had a noticeable effect on the distribution of the F_2 offspring. There seemed to be a slight tendency for the slower F_1's to produce slower offspring, but on the whole the results were quite uniform. However, the faster F_1 parents were found to have produced

[5] The father was removed from the pen before he could influence the young.

proportionately slightly more of the tested F_2 population than were produced by the slower F_1 parents.

F_2 generation

All of the F_2 population which reached 75 days of age was tested in the runway. Segregation of the general behavior of the mice was quite apparent from observation as well as from results of the test. Animals were often found in the same litter which reacted very differently when picked up and examined in the hand.

Table 2 and figures 1 and 2 show the F_2 distribution for the average of three trials in the runway. As can be seen there is a very wide spread, ranging from almost as fast as the fastest grandparents to slower than the slowest grandparent. The distribution was considerably skewed toward the left as was the case in the F_1. The mean, however, occupied a position which was intermediate between that of the F_1 and that of the tame although the average F_2 was not as slow as the parental average. A significant increase in variability was obtained in the F_2 over that in the F_1, showing that considerable segregation had taken place (table 4). There was only one prominent mode in the F_2 distribution. The sexes did not show a significant difference, at least when the difference between the means was compared to the probable error (table 3). The data in this respect were similar to those of the F_1's. Recombinations of other characters with wildness or tameness are discussed under indications of linkage (page 310).

Backcrosses

The results of testing offspring from backcross matings to the wild and tame parental strains are given in table 7. It will be noted that there is a great difference in the distribution of the young from the two types of matings. These distributions were in accord with expectation in that the population of the backcross to the dominant wild lay entirely within the range occupied by the wild and F_1's and was very uniform. Also the population of the backcross to the recessive tame extended from the F_1 range to the tame range and was very variable.

However, it will be noticed that the distribution of the backcross to the wild is extremely skewed toward the wild and that in the distribution of the backcross to the tame none of the individuals are as fast as the fastest F_1's while the slowest are slower than the slowest parent used. Heterozygosity for the factors for a slow reaction in the tame parent together with the difference between the tame individuals used in the original cross with the wild and those used in the backcross would account for these discrepancies. Tame mice from the first generation were used in the original cross, while individuals of the second and third generation were largely used for the backcross.

In addition to the above, results from progeny tests on females in backcrosses to tame males were also obtained. From matings of this type one would expect the offspring of different females to vary in degrees of wildness from that of the mother to that of the father. In most cases the speed of the fastest offspring approximated the speed of the mother (table 8). However, the four slowest females did produce some young considerably faster than themselves and three of the seven males used produced some offspring slower than themselves. These unexpected deviations may be accounted for by a number of suppositions such as inaccuracy of the test, presence of complementary factors or the occurrence of some dominant genes for the reaction in the tame males. (These must be modifying genes.) The latter explanation appears to be the best in view of the results obtained by selection within the tame stock.

F_2 and F_3 selections

The results of selecting and mating F_2's and F_3's having different reactions in the runway in an attempt to establish strains that would breed true are given in table 9. It will be noted that the offspring from the first mating given are all within the limits of the original wild stock. Also a mating of two of these offspring, the first mating given for the F_3's, produced offspring all of which were also within the limits of the original wild strain. The offspring from all the other matings showed considerable variation. In general, though, the slower the parents were the slower the offspring. None of the offspring of the slowest parents were within the range of the wild. The small number of offspring from many of these matings made it impossible to consider the results from them conclusive.

Selection in the wild and tame stocks

Table 10 and figures 3 and 4 give the means for four generations of selection on the wild and tame stocks. In the wild strain the fastest individuals were selected, while in the tame strain the slowest were selected for breeders. It is clearly evident that selection had a marked effect on the tame strains. This progress towards a slower reaction by means of selection shows clearly that the original tame stocks were probably heterozygous for modifying factors for the reaction. (The tame mice must of necessity be homozygous for the recessive allelomorph of the principal gene or genes controlling wildness; otherwise they would be wild like the F_1's.) This has also been shown in the F_2 and backcrosses to the tame where progeny slower than the tame parent were produced. On the other hand,

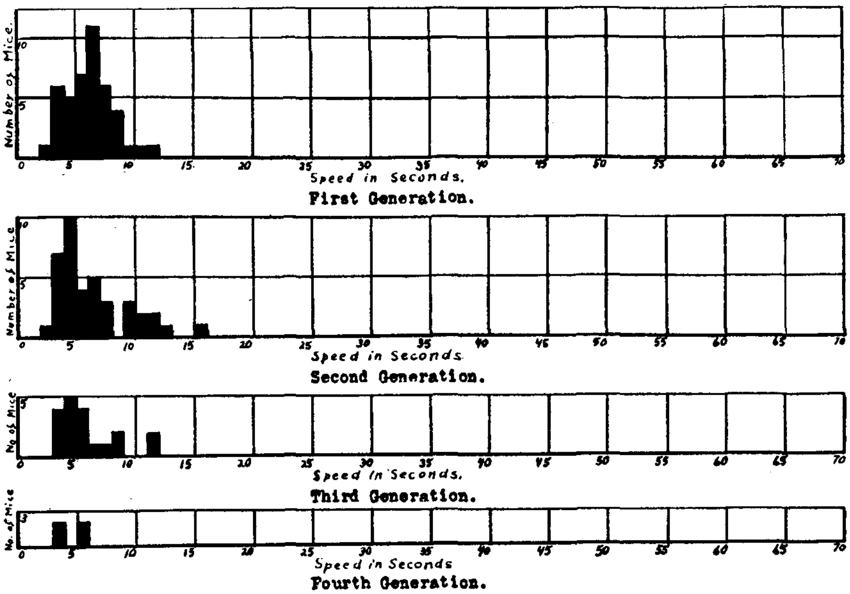


FIGURE 3a.—Distribution of wild males in succeeding generations of selection for wildness. Average of three trials.

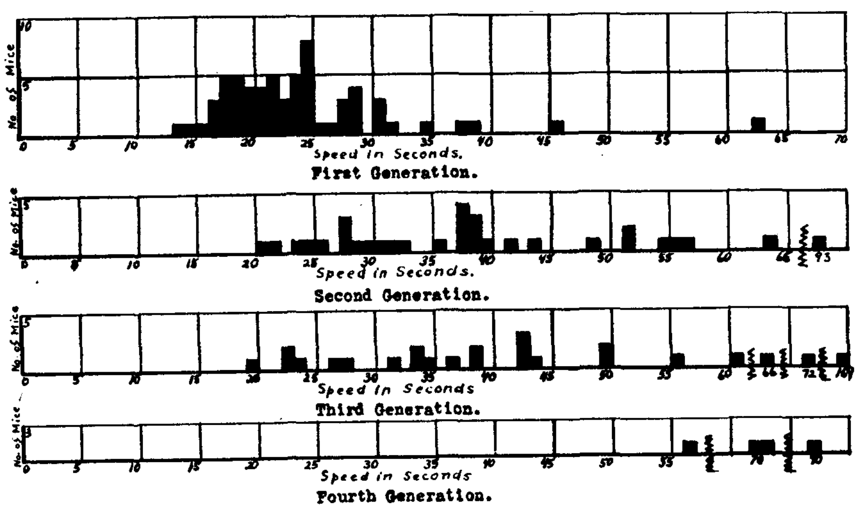


FIGURE 3b.—Distribution of tame males in succeeding generations of selection for tameness. Average of three trials.

selection seems to have had very little effect on the wild strain. Since wildness proved to be almost completely dominant over tameness, it would take a long time to produce any effect by selection even with heterozygous individuals present in the population. Selection of the fastest indi-

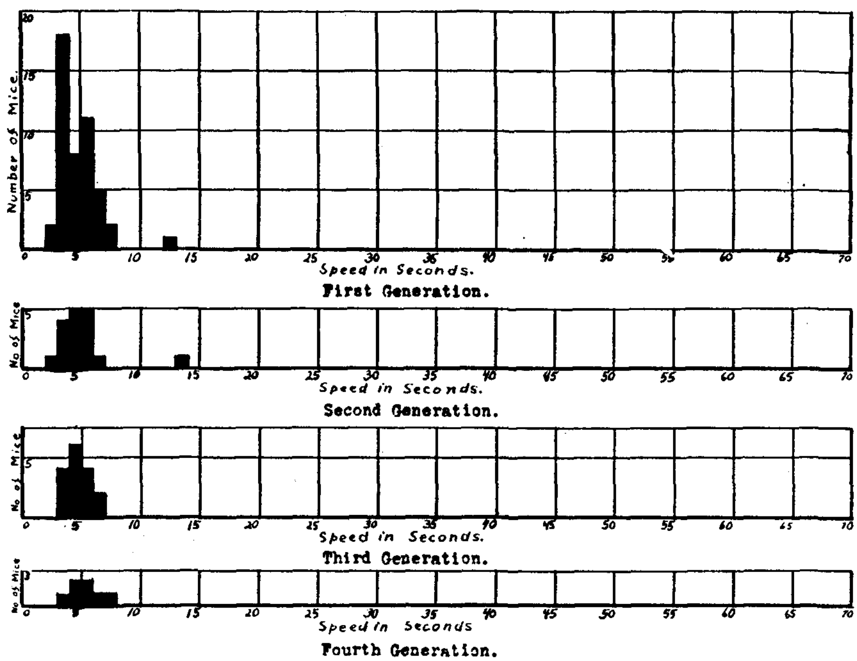


FIGURE 4a.—Distribution of wild females in succeeding generations of selection for wildness. Average of three trials.

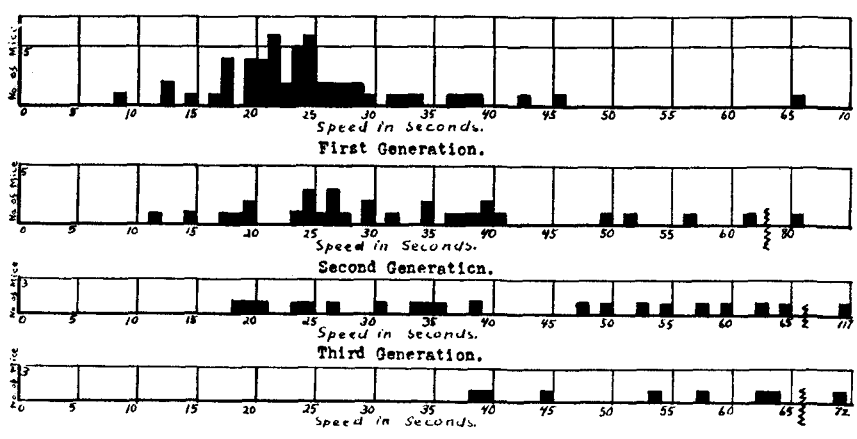


FIGURE 4b.—Distribution of tame females in succeeding generations of selection for tameness. Average of three trials.

viduals for breeders and the elimination of any recessives which might appear could be expected to produce a more homozygous population for the genes which cause the mice to run fast by the gradual reduction of the number of heterozygous individuals present. It might not be possible to demonstrate this effect except by breeding tests unless large numbers were used. The fact that the wild had been subjected for many generations to natural selection would lead one to expect them to be homozygous for all or nearly all the factors which would cause the mice to run quickly in the runway.

Indications of linkage

The data from the F_2 and backcrosses to the tame have been analyzed for indications of linkage by comparing the means of the groups showing the recessives albinism, brown, pink eye, non-agouti, and short ear with the mice having the normal allelomorph of the character in question. The results from the F_2 are given in table 11, those from the backcross in table 12. It can be seen that if any linkage existed it was slight. The differences which appeared to be significant in the F_2 did not show the same relationship in the backcross. Since there were no pink eyed short eared browns in the backcross and since the F_2 population was not separated into strains, a direct comparison in this way is subject to error. Further work along this line might be profitable when larger numbers are involved and the experiment is planned to test linkage.

From table 11 it appeared that the number of recessive genes present might have an effect on the reaction of the individual. When groups of F_2's homozygous for one, two or three of the recessive genes non-agouti, brown and pink eye were studied, the individuals with the most recessives seemed to be somewhat slower than individuals having the dominant allelomorphs. More data, however, would be necessary for definite conclusions.

Estimation of the number of genetic factors

An attempt has been made to estimate the number of genetic factors responsible for the results obtained in the runway. The fact that parental types were so quickly obtained in the F_2 with such a small population would indicate that the greater part of the difference between the wild and the tame strains is due to relatively few genes. However, the response to selection in the tame, the extreme skewness of the distribution in the F_2 and the lack of distinct modes in the backcross to the tame indicate that while a few genes may largely control the response of the individual yet a rather large number have some influence.

In attempting to determine the number of genes which largely control the response of the animal, the population of the second generation of wild and tame strains, F_1's and the backcrosses to the wild and tame have been given values proportionate to their occurrence as genotypic types in the F_2 when Mendelian ratios for one, two and three gene differences are taken. The second generation of the wild and tame strains was used because it would show the effect that selection could be expected to play in the original cross. The combination of the wild, F_1 and tame populations in the proportion $\frac{1}{4}+\frac{1}{2}+\frac{1}{4}$ should give the expected F_2 distribution for a one factor difference. If the parent types were pure this could be expected to approximate closely the observed. For a two factor difference the backcrosses to the tame and wild can be used to supply the distribution of classes not given by the parental or F_1 strains. Because dominance is so nearly complete it can be assumed that classes such as *aaBB* and *aaBb* are practically identical. When more than two or three factors are assumed to have any considerable effect, these classes, accounted for by the assumption of dominance, become more important and where dominance is not complete probably sufficient error is introduced to make it impractical to use the method.

The distributions expected in the F_2 are shown in figures 5, 6 and 7, when one, two and three gene differences are involved. The method of adding together the components which make up the F_2 population as described above was used. The actual F_2 distribution is also given and a comparison of the means of the two curves made.

The probability that the difference between the means was due to chance was greatest when a difference of two genes was used as the basis of the expected F_2 distribution. When the χ^2 test for goodness of fit was used the probability that the difference between the curves was due to chance was very low in all cases. The best fits were secured when a difference of two genes was used in the males and when a difference of three genes was used in the females. It should be noted, however, that the general shape of the expected curve seems to correspond somewhat better when a difference of one gene was used than when two or three genes were used in the case of the males. A satisfactory explanation for this has not been discovered.

In each of the three cases the expected F_2 distribution has more individuals at the extremes and less in the region from about eight to fourteen seconds than the actual F_2 population. The region from eight to fourteen seconds in the expected F_2 distribution is made up almost entirely of F_1's, the slowest individuals from the backcross to the wild and the fastest individuals from the backcross to the tame.

An examination of the backcross distributions shows in both cases that there are fewer individuals within the range eight to fourteen seconds than would be expected if the backcross had produced all classes in equal proportion. Theoretically, the fastest individuals from the backcross to the tame should coincide with the fastest F_1's while the slowest individuals from the backcross to the wild should coincide with the slowest F_1's if the

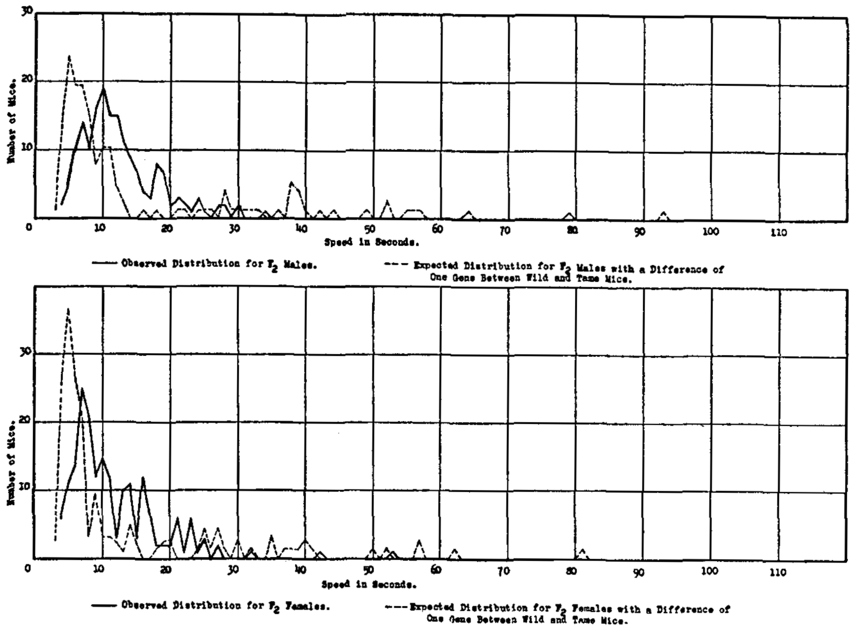


FIGURE 5.—Comparison of the observed F_2 distributions for males and females with those expected for a difference of one gene between the wild and tame mice.

In the expected F_2 distribution the wild second generation $=1/4$, the $F_1=1/2$, the tame second generation $=1/4$.

The means for the distributions were:

	Males	*Females*
Expected	15.985 ± 0.576	13.413 ± 0.701
Observed	12.949 ± 0.387	11.853 ± 0.331
Difference	3.036 ± 0.694	1.560 ± 0.775
Diff./P.E.	4.4	2.6

parental stocks used in the original cross and in the backcrosses were of the same genetic constitution. The fact that the overlap between the wild and tame backcrosses covers a somewhat less extended range than the distribution of the F_1's (tables 2 and 7) suggests that the parental stocks used in the original cross and those used in the backcrosses did differ genetically. Under these conditions a divergence of the expected and actual F_2 distributions would be expected.

If heterozygosity is introduced in one of the parents, as for example a cross between $AABB \times Aabb$, the F_1's will consist of two types which if dominance is present will be very similar to the dominant parent and to each other. Random matings between these two types, however, would give in the F_2, instead of a 9:3:3:1 ratio, a ratio of 45:15:3:1. If the population were not very large this would appear like a 3:1 ratio with perhaps one or two exceptional individuals. With three pairs involved and one pair heterozygous in the recessive parent, as for example in the mating $AABBCC \times Aabbcc$ the F_1 would still have two types and the F_2 would give a ratio of 135:45:45:15:9:3:3:1 assuming dominance. If the population were small the bulk of this distribution could be expected to re-

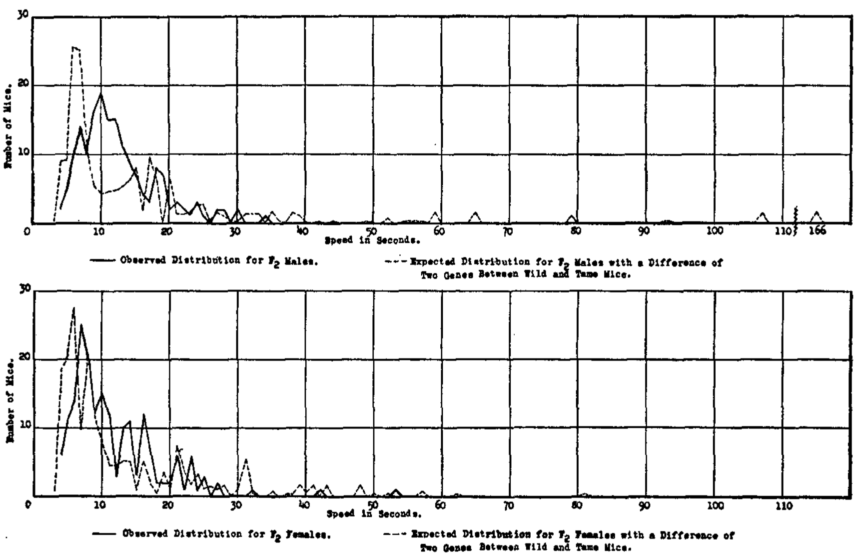


FIGURE 6.—Comparison of the observed F_2 distributions for males and females with those expected for a difference of two genes between the wild and tame mice.

In the expected F_2 distribution the wild second generation = 1/16, the $F_1 \times$wild (F_1 = 1/4 + wild = 1/4) = 1/4, the F_1 = 1/4, the $F_1 \times$tame (F_1 = 1/4 + tame = 1/4) = 3/8, the tame second generation = 1/16.

The means for the distributions were:

	Males	*Females*
Expected	16.348±1.052	13.007±0.542
Observed	12.949±0.387	11.853±0.331
Difference	3.399±1.122	1.154±0.636
Diff./P.E.	3.0	1.8

semble a 9:3:3:1 ratio. From these examples it can be seen that the introduction of heterozygosity in the parents lowers the gametic differences and therefore will cause the F_2 population in similar cases to appear to have a lower number of genes involved than is actually the case.

The above discussion is based upon the assumption that there is equal viability for the gametes from the different F_1 types. In case there is a difference, as, for example, if the gametes from *AABb* were more viable than those for *AaBb*, then the resulting distribution would approach that

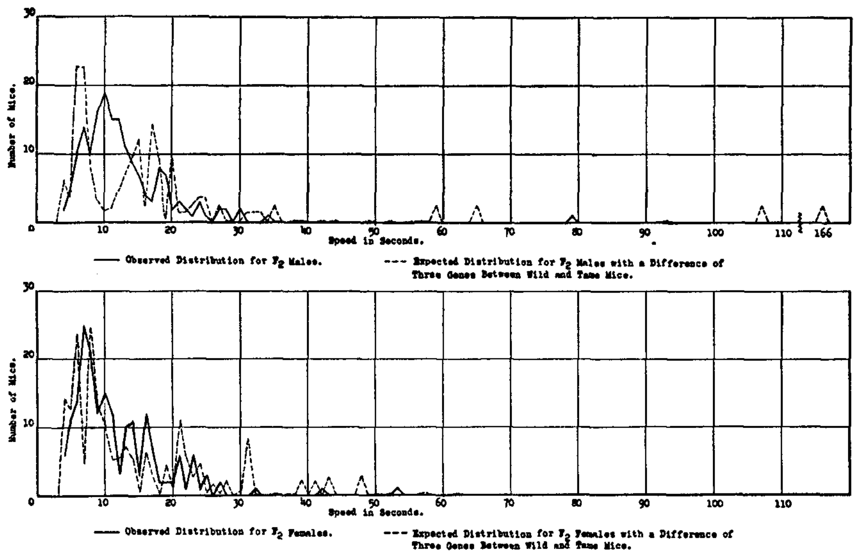


FIGURE 7.—Comparison of the observed F_2 distributions for males and females with those expected for a difference of three genes between the wild and tame mice.

In the expected F_2 distribution the wild second generation = 1/64, the $F_1 \times$ wild (F_1 = 1/8 + wild = 1/8) = 18/64, the F_1 = 1/8, the $F_1 \times$ tame (F_1 = 1/8 + tame = 1/8) = 36/64, the tame second generation = 1/64.

The means for the distributions were:

	Males	*Females*
Expected	18.760±1.208	14.018±0.510
Observed	12.949±0.387	11.853±0.331
Difference	5.811±1.268	2.165±0.608
Diff./P.E.	4.6	3.6

of a single factor difference more nearly than if the viability were equal. On the other hand, if the gametes from *AaBb* were the more viable the distribution would approximate more closely the distribution for a two factor difference.

The effect of unequal numbers of the different types in the F_1 would be similar to that for unequal viability of the gametes.

Applying the above reasoning to the results from the runway tests the following appear probable:

1. That there are two or three genes involved that have considerable influence on the reaction.[6]

2. That practically all the wild parents were homozygous for the dominant genes.

3. That most of the tame parents were homozygous for at least two recessive genes and heterozygous for the other.

4. That the unequal fertility noted in the F_1's coupled with the heterozygosity of one or more pairs of genes in the tame parent has caused the distribution of the F_2 to be skewed somewhat more toward the left than it would be otherwise.

5. That the variation from the distribution expected with a difference of two genes is compatible with the results of selection in the tame strains.

DISCUSSION

A number of other experimenters have attempted to study the inheritance of wildness and tameness or characters of a somewhat similar nature. The results obtained in the present investigation, in spite of differences in methods and materials, agree at least in certain respects with those of YERKES (1913) and COBURN (1922), both of whom found wildness and tameness to be inherited and that wildness was largely dominant over tameness, and also those of VICARI (1929) who, in studying the inheritance of reaction time and degrees of learning in mice, found that where there was a wide difference between short and long reaction time some form of dominance of the short reaction time was evident. Others who have studied the inheritance of characters of this type are BAGG (1920), TOLMAN (1924) and SADOVNIKOVA-KOLTZOVA (1926). Their results all give some evidence that inheritance affects the characters studied but, at least from the data presented, appear to give very little information on the mode of inheritance.

SUMMARY AND CONCLUSIONS

Whether the characters wildness and tameness in mice as measured by the results of testing in the runway are inherited was studied by making

[6] CASTLE (1921) has proposed a formula ($n = D^2/8[\sigma_2^2 - \sigma_1^2]$) for estimating the number of genes concerned in cases of blending inheritance. While the application of this formula to the present material may be questioned, yet it is interesting to note that the estimated number of genes arrived at by this method is 2.6 for the males and 2.7 for the females, when D in the above formula equals the difference between the mean of the wild second generation and the mean of the tame second generation (see third paragraph, page 311).

appropriate crosses. One strain of wild mice and three strains of tame mice were used in the experiment. That factors for wildness and tameness are inherited is shown by the following:

1. A distinct difference was found between the wild and tame stocks. This difference was increased by selecting the parents through four generations.
2. The F_1 offspring were very nearly as fast as the wild parent.
3. The results of mating F_1's back to the wild stock were very different from those obtained by mating the F_1's to the tame stock.
4. Segregation similar to that of other characters which are inherited was obtained when the F_1's were mated *inter se* and to the tame stock.
5. The association of the young with the mother had no effect on their reaction when tested in the runway.

As to the mode of inheritance of the genes controlling the characters wildness and tameness, the most important facts disclosed are:

1. Only a few genes appear to influence the reaction to any great extent.
2. The genes which are responsible for wildness seem to be almost completely dominant to those which are responsible for tameness.
3. There is very little evidence from the results that any of these genes are linked with sex.
4. There is very little evidence that there is any linkage between these genes and those for albinism, pink eye, agouti, brown, or short ear.
5. Continued selection showed that probably a number of modifying genes are present.

LITERATURE CITED

Bagg, H. J., 1920 Individual differences and family resemblances in animal behavior. Arch. Psychol. New York **26**: 58.

Castle, W. E., 1921 An improved method of estimating the number of genetic factors concerned in cases of blending inheritance. Science **54**: 223.

Coburn, C. A., 1922 Heredity of wildness and savageness in mice. Behav. Monog. **4**: 1–71.

Kelley, T. L., 1923 Statistical method. New York: The Macmillan Co.

Odell, C. W., 1930 Educational measurement in high school. New York: The Century Co.

Rietz, H. L., 1927 Mathematical statistics. Chicago: Open Court Publishing Co.

Sadovnikova-Koltzova, M. P., 1926 Genetic analysis of temperament of rats. J. Exp. Zool. **17**: 342–359.

Shen, E., 1924 The standard error of certain estimated coefficients of correlation. J. Educ. Psychol. **15**: 462–465.

Tolman, E. C., 1924 The inheritance of maze ability in rats. J. Comp. Psychol. **4**: 1–18.

Vicari, E. M., 1929 Mode of inheritance of reaction time and degrees of learning in mice. J. Exp. Zool. **54**: 31–88.

Yerkes, R. M., 1913 The heredity of savageness and wildness in rats. J. Anim. Behav. **8**: 286–296.

TABLE 2

Distribution of the first generation wild, first generation tame, F_1's and F_2's in runway test. Average of three trials.

SPEED IN SECONDS	MALES				FEMALES			
	WILD FIRST GENERATION	TAME FIRST GENERATION	F_1's	F_2's	WILD FIRST GENERATION	TAME FIRST GENERATION	F_1's	F_2's
3	1	..	..	..	2	..	..	..
4	6	..	6	2	18	..	14	6
5	5	..	11	5	8	..	21	11
6	7	..	13	10	11	..	12	14
7	11	..	12	14	5	..	17	25
8	6	..	10	10	2	..	3	21
9	4	..	7	16	..	1	9	12
10	1	..	6	19	..	..	3	15
11	1	..	7	15	..	..	3	12
12	1	..	2	15	..	..	1	3
13	..	..	1	11	1	2	1	10
14	..	1	..	9	..	..	2	11
15	..	1	..	7	..	1	1	3
16	..	1	..	4	..	..	..	12
17	..	3	..	3	..	1	..	7
18	..	5	1	8	..	4	..	2
19	..	5	..	7	..	..	1	2
20	..	4	..	2	..	4	..	2
21	..	4	..	3	..	4	..	6
22	..	5	..	2	..	6	..	1
23	..	3	..	1	..	2	..	6
24	..	5	..	3	..	5	..	1
25	..	8	..	1	..	6	..	3
26	..	1	..	..	..	2	..	..
27	..	1	..	2	..	2	..	2
28	..	3	..	2	..	2	..	..
29	..	4	..	..	..	2	..	..
30	..	..	..	2	..	1	..	..
31	..	3	..	..	..	..	..	..
32	..	1	..	..	..	1	..	1
33	..	..	..	..	..	1	..	..
34	..	..	..	1	..	1	..	..
35	..	1	..	..	..	..	..	..
36	..	..	..	..	..	..	..	..
37	..	..	..	..	..	1	..	..
38	..	1	..	..	..	1	..	..
39	..	1	..	..	..	1	..	..
40	..	..	..	..	..	..	..	..
41	..	..	..	..	..	..	..	..
42	..	..	..	..	..	..	..	1
43	..	..	..	..	..	1	..	..
46	..	1	..	..	..	1	..	..
53	..	..	..	..	..	..	..	1
63	..	1	..	..	..	..	..	..
66	..	..	..	..	..	1	..	..
79	..	..	..	1	..	..	..	..
Total	43	63	76	175	47	54	88	190
Mean	6.698 ±0.202	24.492 ±0.654	7.579 ±0.198	12.949 ±0.387	5.277 ±0.167	25.352 ±0.825	6.898 ±0.203	11.853 ±0.331

TABLE 3

Comparison of wildness of males and females in the wild first generation, tame first generation, F_1's and F_2's in the runway test. Average of three trials.

STRAIN	TRIAL	NO. OF IND.	MEAN FOR MALES	NO. OF IND.	MEAN FOR FEMALES	DIFFERENCE	D/P.E.
Wild	1	43	8.116±0.298	47	6.000±0.193	2.116±0.355	6.0
Wild	2	43	6.302±0.221	47	4.936±0.207	1.366±0.303	4.5
Wild	3	43	5.651±0.189	47	4.660±0.174	0.991±0.257	3.9
Wild	Average	43	6.698±0.202	47	5.277±0.167	1.421±0.263	5.4
Albino	1	39	31.436±0.872	41	36.732±0.127	5.296±0.881	6.0
Albino	2	39	19.385±0.506	41	18.976±0.717	0.409±0.877	0.5
Albino	3	39	16.154±0.502	41	15.829±0.565	0.325±0.756	0.4
Albino	Average	39	22.359±0.486	41	23.927±0.760	1.568±0.902	1.7
Pink-eyed short eared brown	1	20	38.650±2.209	11	45.727±5.148	7.077±5.602	1.3
	Average 3 Trials	20	27.900±1.525	11	31.182±2.566	3.282±2.985	1.1
Pink eyed brown	Average 3 Trials	4	28.250±3.492	2	22.500±0.239	5.750±3.500	1.6
All Tame	Average 3 Trials	63	24.492±0.654	54	25.352±0.825	0.860±1.054	0.8
F_1's	Average 3 Trials	76	7.579±0.198	88	6.898±0.203	0.680±0.284	2.4
F_2's	Average 3 Trials	175	12.949±0.387	190	11.853±0.331	1.096±0.510	2.1

TABLE 4

Comparisons of the means and standard deviations for various groups, average of three trials.

GROUP	NUMBER OF INDIVIDUALS	MEAN SPEED	GROUP	NUMBER OF INDIVIDUALS	MEAN SPEED	DIFFERENCE	D/P.E.
Wild first generation ♂♂	43	6.70±0.20	Tame first generation ♂♂	63	24.49±0.65	17.79±0.68	26.2
Wild first generation ♀♀	47	5.28±0.17	Tame first generation ♀♀	54	25.35±0.82	20.07±0.84	24.0
Wild first generation ♂♂	43	6.70±0.20	F_1 ♂♂	76	7.58±0.20	.88±0.28	3.1
Wild first generation ♀♀	47	5.28±0.17	F_1 ♀♀	88	6.90±0.20	1.62±0.26	6.2
Tame first generation ♂♂	63	24.49±0.65	F_1 ♂♂	76	7.58±0.20	16.91±0.68	24.9
Tame first generation ♀♀	54	25.35±0.82	F_1 ♀♀	88	6.90±0.20	18.45±0.84	22.0
F_1 ♂♂	76	7.58±0.20	F_2 ♂♂	175	12.95±0.39	5.37±0.44	12.2
F_1 ♀♀	88	6.90±0.20	F_2 ♀♀	190	11.85±0.33	4.95±0.39	12.7
		Standard deviation			Standard deviation		
Wild first generation ♂♂	43	1.96±0.14	Tame first generation ♂♂	63	7.70±0.46	5.74±0.48	12.0
Wild first generation ♀♀	47	1.70±0.12	Tame first generation ♀♀	54	8.99±0.58	7.29±0.59	12.4
Wild first generation ♂♂	43	1.96±0.14	F_1 ♂♂	76	2.55±0.14	.59±0.20	3.0
Wild first generation ♀♀	47	1.70±0.12	F_1 ♀♀	88	2.82±0.14	1.12±0.18	6.2
Tame first generation ♂♂	63	7.70±0.46	F_1 ♂♂	76	2.55±0.14	5.15±0.48	10.7
Tame first generation ♀♀	54	8.99±0.58	F_1 ♀♀	88	2.82±0.14	6.17±0.60	10.3
F_1 ♂♂	76	2.55±0.14	F_2 ♂♂	175	7.59±0.27	5.04±0.30	16.8
F_1 ♀♀	88	2.82±0.14	F_2 ♀♀	190	6.77±0.23	3.95±0.26	15.2

TABLE 5

Distribution of wild and albino tame strains in the first, second and third trials.

SPEED IN SECONDS	MALES						FEMALES					
	WILD FIRST GENERATION			ALBINO TAME FIRST GENERATION			WILD FIRST GENERATION			ALBINO TAME FIRST GENERATION		
	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL
3	1	2	4	..	..	..	2	10	14	..	..	..
4	3	9	9	..	..	..	8	16	12	..	..	..
5	5	6	8	..	..	..	12	9	9	..	..	..
6	5	6	10	..	..	..	11	3	7	..	..	1
7	4	10	7	..	..	..	5	6	3	..	..	1
8	7	4	3	..	..	..	3	1	..	..	1	1
9	5	3	..	..	..	..	4	..	1	..	1	2
10	6	1	1	..	1	2	1	..	..	1	..	..
11	3	1	..	..	..	5	..	1	..	..	1	6
12	1	..	1	..	1	3	..	..	1	1	2	2
13	..	1	..	..	1	4	1	..	..	..	1	3
14	1	..	..	..	3	4	..	1	..	..	4	2
15	1	..	..	..	1	1	..	..	..	..	3	1
16	1	..	..	..	6	4	..	..	..	..	3	3
17	..	..	..	..	3	4	..	..	..	..	3	3
18	..	..	..	1	1	..	..	..	..	..	3	3
19	..	..	..	1	5	2	..	..	..	..	3	6
20	..	..	..	1	2	2	..	..	..	1	4	..
21	..	..	..	1	3	4	..	..	..	..	2	1
22	..	..	..	2	2	1	..	..	..	..	2	1
23	..	..	..	2	3	1	..	..	..	2	2	..
24	..	..	..	1	2	..	..	..	..	..	..	3
25	..	..	..	2	..	..	..	..	..	1	2	..
26	..	..	..	1	..	..	..	..	..	2	..	1
27	..	..	..	2	2	..	..	..	..	..	..	..
28	..	..	..	1	1	1	..	..	..	..	..	..
29	..	..	..	3	2	1	..	..	..	1	1	..
30	..	..	..	..	..	..	..	..	..	1	1	1
31	..	..	..	3	..	..	..	..	..	4	..	..
32	..	..	..	2	..	..	..	..	..	1	..	..
33	..	..	..	1	..	..	..	..	..	1	..	..
34	..	..	..	2	..	..	..	..	..	1	..	..
35	..	..	..	1	..	..	..	..	..	5	..	..
36	..	..	..	2	..	..	..	..	..	..	..	..
37	..	..	..	..	..	..	..	..	..	1	..	..
38	..	..	..	2	..	..	..	..	..	..	1	..
39	..	..	..	..	..	..	..	..	..	2	..	..
40	..	..	..	3	..	..	..	..	..	..	..	..
41	..	..	..	..	..	..	..	..	..	5	..	..
42	..	..	..	..	..	..	..	..	..	1	..	..
43	..	..	..	1	..	..	..	..	..	2	1	..

TABLE 5 (continued)

SPEED IN SECONDS	MALES						FEMALES					
	WILD FIRST GENERATION			ALBINO TAME FIRST GENERATION			WILD FIRST GENERATION			ALBINO TAME FIRST GENERATION		
	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL	FIRST TRIAL	SECOND TRIAL	THIRD TRIAL
44	..	..	..	1	..	..	..	..	..	..	..	..
45	..	..	..	1	..	..	..	..	..	..	..	..
46	..	..	..	1	..	..	..	..	..	2	..	..
47	..	..	..	..	..	..	..	..	..	2	..	..
50	..	..	..	1	..	..	..	..	..	..	..	..
55	..	..	..	..	..	..	..	..	..	1	..	..
61	..	..	..	..	..	..	..	..	..	1	..	..
66	..	..	..	..	..	..	..	..	..	1	..	..
68	..	..	..	..	..	..	..	..	..	1	..	..
Total	43	43	43	39	39	39	47	47	47	41	41	41
Mean	8.116	6.302	5.651	31.436	19.385	16.154	6.000	4.936	4.660	36.732	18.976	15.829
	±0.298	±0.221	±0.189	±0.872	±0.506	±0.502	±0.193	±0.207	±0.174	±0.127	±0.717	±0.565

TABLE 6

Comparison of the F_1's from reciprocal crosses in the runway test using the means of the populations.

PARENTS	MEANS OF F_1'S	
	MALES	FEMALES
Wild male × tame female	7.740±0.270	6.714±0.240
Tame male × wild female	7.120±0.167	7.360±0.374
Difference	0.620±0.317	0.646±0.444
Diff./P.E.	1.956	1.455

TABLE 7

Distribution in backcrosses in runway test average of three trials.

SPEED IN SECONDS	BACKCROSS TO WILD		BACKCROSS TO TAME	
	MALES	FEMALES	MALES	FEMALES
4	3	5	..	..
5	2	5	..	..
6	8	8	1	1
7	8	1	1	..
8	3	4	1	4
9	1	..	..	5
10	..	..	1	4
11	..	..	1	2
12	1	..	2	2
13	..	..	3	3
14	..	..	4	2
15	..	..	5	..
16	..	1	1	1
17	..	..	6	1
18	..	..	4	..
19	..	..	..	2
20	..	..	4	1
21	..	..	1	4
22	..	..	1	2
23	..	..	1	1
24	..	..	2	2
25	..	..	2	1
26	..	..	..	1
27	..	..	1	..
28	..	..	1	1
29	..	..	..	..
30	..	..	..	1
31	..	..	1	3
32	..	..	1	..
33	..	..	1	..
34	..	..	..	..
35	..	..	1	..
36	..	..	..	..
37	..	..	..	..
38	..	..	1	..
39	..	..	..	1
40	..	..	..	..
41	..	..	..	1
43	..	..	..	1
48	..	..	...	1
59	..	..	1	..
65	..	..	1	..
92	..	..	1	..
96	..	..	1	..
107	..	..	1	..
166	..	..	1	..
Total	26	24	54	48
Mean	6.577±0.217	6.167±0.334	27.389±2.589	18.729±0.993

TABLE 8

Distribution of progeny from backcross (F_1 ♀ × tame ♂) and double backcross ([F_1 ♀ × tame ♂] ♀ × tame ♂) females mated to tame males. Runway test. Average of three trials.

Sire Speed	1352 42.6						1349 42.6			2090 57.0	1716 60.8					2356 70.3	2124 71.2	2355 89.5	
Dam Speed	1650 8.5	1649 11.3	1648 13.1	1659 21.1	1651 21.6	1829 40.9	1745 8.1	1738 8.3	1744 11.1	1822 46.6	1745 8.1	1743 8.1	1738 8.3	1742 8.4	1697 19.5	2102 9.8	2204 17.9	2371 32.0	2332 51.4
Speed of Male Offspring	8	22	21	22	28	26	15	12	19	..	..	47	30	32	20	12	40	59	49
	9	24	48	46	56	31	40	..	25	..	..	58	..	56	23	20	45	..	..
	11	31	53	..	61	..	46	..	33	..	..	100	..	67	24	21	61	..	..
	13	35	69	..	..	..	..	..	33	..	..	..	..	..	25	25	..	..	..
	22	37	..	..	..	..	..	..	..	..	..	..	..	..	27	31	..	..	..
	24	46	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	62	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Average	14.5	36.7	47.8	34.0	48.3	28.5	33.7	12.0	27.5			68.3	30.0	51.7	23.8	21.8	48.7	59.0	49.0
Speed of Female Offspring	7	9	18		22	9	11	8	15	28	14	21	9	18	20	24	29	22	24
	8	14	23		30	43	23	10	27	28	43	28	..	51	22	..	45	26	..
	9	17	26		35	..	34	14	28	36	..	34	..	..	34	..	57	33	..
	13	19	41		51	..	36	17	46	43	..	..	..	..	..	..	59	40	..
	14	25	..		..	..	58	..	..	..	..	..	..	..	..	..	..	..	..
	19	33	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	25	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	26	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	30	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	31	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	32	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	46	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	47	..	..		..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Average	23.6	19.5	27.0		34.5	26.0	32.4	12.2	29.0	33.8	28.5	27.7	9.0	34.5	25.3	24.0	47.5	30.2	24.0
Grand Average	20.7	28.8	37.4	34.0	40.4	27.2	32.9	12.2	28.2	33.8	28.5	48.0	19.5	44.8	24.4	22.2	48.0	36.0	36.5

NOTE: 2204, 2371 and 2332 are (F_1×tame)×tame. The others are F_1×tame.

TABLE 9

Results of selecting and mating F_2's and F_3's of different degrees of wildness and tameness. Runway test.

MEAN SPEED OF F_2 PARENTS	NUMBER OF YOUNG		RANGE		AVERAGE SPEED	
	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES
4.2	4	4	4–5	4–6	4.8	4.8
5.8	5	6	7–11	5–9	8.4	7.0
6.2	4	6	7–44	8–37	20.8	21.2
9.1	2	3	7–27	5–6	17.0	5.7
9.5	14	14	9–18	6–36	13.9	13.5
11.4	13	25	11–44	5–31	20.8	17.9
20.4	1	5	8	10–15	8.0	13.4
26.1	..	1	..	50	..	50.0
Mean Speed of F_3 Parents						
4.3	8	3	4–9	6–8	5.6	7.3
18.6	9	7	13–42	11–23	22.8	17.3
31.6	10	6	19–50	23–38	31.7	30.8
40.5	7	3	38–205	42–56	71.3	48.7

TABLE 10

Results of selection on wild and tame stocks. Runway test. Average of three trials.

STOCK	GENERATION	MEAN	GENERATION	MEAN	DIFFERENCE	D/P.E.
Wild ♂♂	1	6.698±0.202	2	6.897±0.097	+0.199±0.224	0.9
Wild ♂♂	1	6.698±0.202	3	6.421±0.377	−0.277±0.428	0.6
Wild ♂♂	1	6.698±0.202	4*	5.000±0.377	−1.698±0.394	4.3
Wild ♂♂	2	6.897±0.097	3	6.421±0.377	−0.476±0.389	1.2
Wild ♂♂	2	6.897±0.097	4	5.000±0.337	−1.897±0.351	5.4
Wild ♂♂	3	6.421±0.377	4	5.000±0.337	−1.421±0.506	2.8
Wild ♀♀	1	5.277±0.167	2	5.588±0.381	+0.311±0.416	0.7
Wild ♀♀	1	5.277±0.167	3	5.250±0.163	−0.027±0.233	0.1
Wild ♀♀	1	5.277±0.167	4	5.857±0.318	+0.580±0.359	1.6
Wild ♀♀	2	5.588±0.381	3	5.250±0.163	−0.338±0.415	0.8
Wild ♀♀	2	5.588±0.381	4	5.857±0.318	−0.269±0.496	0.5
Wild ♀♀	3	5.250±0.163	4	5.857±0.318	+0.607±0.358	1.7
Tame ♂♂	1	24.492±0.654	2	39.562±1.736	+15.070±1.855	8.1
Tame ♂♂	1	24.492±0.654	3	45.500±2.849	+21.008±2.923	7.2
Tame ♂♂	1	24.492±0.654	4	72.000±3.969	+47.508±4.022	11.8
Tame ♂♂	2	39.562±1.736	3	45.500±2.849	+5.938±3.336	1.8
Tame ♂♂	2	39.562±1.736	4	72.000±3.969	+32.438±4.332	7.5
Tame ♂♂	3	45.500±2.849	4	72.000±3.969	+26.500±4.886	5.4
Tame ♀♀	1	25.352±0.825	2	34.188±1.782	+8.836±1.964	4.5
Tame ♀♀	1	25.352±0.825	3	44.000±3.382	+18.648±3.481	5.4
Tame ♀♀	1	25.352±0.825	4	54.375±2.696	+29.023±2.819	10.3
Tame ♀♀	2	34.188±1.782	3	44.000±3.382	+9.812±3.822	2.6
Tame ♀♀	2	34.188±1.782	4	54.375±2.696	+20.187±3.231	6.2
Tame ♀♀	3	44.000±3.382	4	54.375±2.696	+10.375±4.324	2.4

* The fourth generation wild males was very small, consisting of only four individuals.

TABLE 11

Analysis of the F_2 population for indications of linkage between wildness and albinism, agouti, brown, pink eye and short ear.

CHARACTER	MALES		FEMALES	
	NUMBER	MEAN	NUMBER	MEAN
Colored	148	11.885±0.300	160	11.012±0.316
Albino	27	18.778±1.706	30	16.333±1.099
Difference		+6.893±1.732		+5.321±1.144
Diff./P.E.		4.0		4.7
Agouti	118	11.941±0.338	134	10.463±0.309
Non Agouti	30	11.667±0.650	26	13.846±1.046
Difference		−0.274±0.732		+3.383±1.090
Diff./P.E.		0.4		3.1
Black	134	11.403±0.280	134	10.381±0.303
Brown	14	16.500±1.458	26	14.269±1.065
Difference		+5.097±1.484		+3.888±1.108
Diff./P.E.		3.4		3.5
Dark eye	127	11.268±0.293	135	9.822±0.268
Pink eye	21	15.619±0.993	25	17.440±1.056
Difference		+4.351±1.035		+7.618±1.090
Diff./P.E.		4.2		7.0
Normal ear	134	11.881±0.321	150	10.753±0.317
Short ear	14	11.929±0.766	10	14.900±1.527
Difference		+0.048±0.831		+4.147±1.559
Diff./P.E.		0.1		2.7

NOTE: The mice were not separated into the strains from which they came. Thus the recessive genes for some characters could not have occurred in the whole population.

TABLE 12

Analysis of the population of the backcross to the tame by strains for indications of linkage between wildness and albinism, agouti, brown and pink eye.

CHARACTER	MALES		FEMALES	
	NUMBER	MEAN	NUMBER	MEAN
MICE FROM ALBINO AND WILD STRAINS*				
Colored	21	23.952±3.166	13	18.077±1.636
Albino	18	33.278±5.838	18	16.056±1.591
Difference		+9.326±6.641		−2.021±2.282
Diff./P.E.		1.4		0.9
Agouti†	15	24.067±4.071	12	15.500±1.935
Non Agouti	6	23.667±4.388	6	17.167±2.770
Difference		−0.400±5.986		+1.667±3.379
Diff./P.E.		0.7		0.5
MICE FROM PINK EYED BROWN AND WILD STRAINS				
Black	5	18.600±1.497	5	15.400±1.765
Brown	7	18.143±1.621	6	29.833±3.394
Difference		−0.457±2.207		+14.433±3.825
Diff./P.E.		0.2		3.8
Agouti	5	14.200±1.327	5	26.600±4.457
Non Agouti	7	21.286±1.232	6	20.500±2.405
Difference		+7.086±1.811		−6.100±5.645
Diff./P.E.		3.9		1.1
Dark eye	6	19.500±1.366	4	20.500±5.446
Pink eye	6	17.167±1.752	7	24.857±2.278
Difference		−2.333±2.222		+4.357±5.903
Diff./P.E.		1.0		0.7

* This does not include mice from F_1 ♀ 544 which was a Detlefsen mutant, apparently introduced through the wild strain.

† Apparently only part of the albino stock carried non agouti.